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THE FAUNAL RELATIONS OF THE EARLY
VERTEBRATES

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VIII

The environmental conditions affecting the evolution of the early air-breathing vertebrates offer at the present time many peculiarly difficult problems, problems which must depend in large measure upon the geologist for solution. They are very different from those which confront the student of the neozoic vertebrates, since we have better data for comparisons and conclusions in the living faunas as well as in our existing climatic and geographic conditions. And especially are the problems more involved and complicated when we attempt to deal with the marine or aquatic air-breathers of those early times. Here we can practically predicate little as to the conditions of the oceans and climates in which they lived. But these early vertebrates do offer, it seems to me, much that is suggestive regarding the migrations and evolution of faunas, involving theories as to paleogeographic conditions and changes, and, within certain limits, the climatic conditions which surrounded and controlled the migrations. And it is of this phase of the subject that I would choose to speak now.

As has been said, the evidence offered by the vertebrates, when available, is often, if not usually, more decisive than that of any other class of organisms in the determination of the relationships and correlations of faunas. A single species of the higher vertebrates

found to occupy two remote provinces would furnish more positive evidence of contemporaneity and the possibilities of faunal migrations than would scores of others of lower types. But of species in vertebrate paleontology we can say little; the term with us is usually a far more vague and indefinite one than it is among students of living faunas, partly because much of the evidence which the neozoölogist has, the paleozoölogist has not, partly because the taxonomy of living creatures is still based too much upon superficial resemblances. And really, for most purposes, genera express in vertebrate paleontology about what species suggest among invertebrates and plants, that is for correlative and evolutionary purposes, at least.

The evolution of vertebrate life, air-breathing vertebrate life, for I shall not presume to speak of the fishes, during Carboniferous times was quite as great as at any subsequent period. Indeed, I think I am quite safe in saying that, so far as the chief problems in vertebrate evolution are concerned, the life of the Carboniferous is the most important of all. From forms scarcely differing from fishes which must have existed at the beginning, of which, alas, we yet have no knowledge, we find evolved at the close forms foreshadowing the chief groups of life of modern times. The predominant types of the Pennsylvanian were what we usually call the branchiosaurs and microsaur, for the most part small or very small creatures, at least as small as their nearest relatives of the present time, the salamanders. We are quite justified in the belief that their habits in general were not greatly unlike these descendants, rather sluggish creatures living about or in the water, for the branchiosaurs at least passed through larval stages. They were more or less protected by an external bodily armor against their enemies, whether of their own or other kinds, in all probability terminating their existence as distinctive types long before the close of the Paleozoic. But among them there were some classed with the heterogeneous group which we call microsaur, which had made a very distinct advance, both toward a higher existence and away from the water. It has been assumed on entirely insufficient evidence that they too were all amphibians, having an early larval existence in the water, but of this we have, for many of them, little or no proof, and there is very little to differentiate the most advanced of them in structure from the reptiles. Some lost the

	CARBONIFEROUS		PERMIAN		TRIAS		JURA		CRETACEOUS		TERTIARY	
	MISS.	PENNA.	L.	U.	L.	M.	U.	L.	LOWER	UPPER	Eocene	Oligocene
PTEROSAURIA		<i>Pterodactylus</i>										
CROCODYLIA		<i>Elanodon</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
DINOSAURIA		<i>Theropoda</i>										
		<i>Sauropoda</i>										
		<i>Protosauropoda</i>										
BIRDS		<i>Saururus</i>										
		<i>Odonatopterus</i>										
		<i>Archaeopteryx</i>										
RHYNCHOCETIDIA		<i>Rhynchocetus</i>										
		<i>Archaeocetus</i>										
		<i>Archaeocetus</i>										
SQUAMATA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
LIGHT HYDRAURIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
POLYLOSAURIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
CHELONIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
ANOMODONTIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
MAMMALS		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
SAUROPTERYGIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
AMPHIBIA		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										
		<i>Phytosaurus</i>										

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dermal armor completely and became fleet of movement, as is evidenced by the structure of their limbs, limbs mimicking in form and in structure so closely those of modern quick-running lizards as to be practically indistinguishable. We may be assured that some of them before the close of the Pennsylvanian were inhabitants of high-and-dry land regions where fleetness of movement, rather than obscurity, preserved them from their enemies, crawling reptiles in everything save some insignificant technical details of their palates. Specialization of the microsaur had reached the extraordinary extent of snake-like limbless forms.

In addition to these two types of land animals we have two others which either persisted from unknown ancestors or made their advent: the temnospondylous type of amphibians from which the mammals eventually arose, and the stereospondylous type which terminated in the gigantic labyrinthodonts of the Upper Trias, the only group of the Pennsylvanian air-breathing vertebrates which we may say with certainty has left no modern descendants behind them. However, till near the close of the Pennsylvanian we have no knowledge of anything distinctive in the American land-vertebrate fauna. There was nothing strikingly peculiar to either eastern or western continent, so far as our knowledge yet extends, and some of the forms, indeed, are almost if not quite identical generically. And the only possible explanation of this homogeneity of types is freedom of communication and migration, the persistence and wide extent of like climatic and freshwater conditions that would permit, for instance, the migration of snake-like forms of small size from Ohio to Ireland and Bohemia without material modification in structure.

However, either the divisional lines between the Pennsylvanian and the Permian have been placed too high, or else, it seems to me, evolution among the vertebrates was more rapid in America than elsewhere near the close of the period. As a continent I believe that the land of America was absolutely and continuously isolated, so far as the intermigrations of land forms was concerned, from some time before the close of the Pennsylvanian till well into Triassic times, as they reckon them in Europe. Of the Permian vertebrates by far the richest and most varied fauna known is that of America, and especially that of Texas and Oklahoma. Professor Case has recently presented

what evidence he could for the Permian age of this fauna and has admittedly failed in proving anything save its utter isolation, and from the evidence we yet have no one can do better than he has done. The fauna was literally *sui generis* and I may almost say *sui ordinis*. But two or three genera of two types out of the scores of genera known from these regions can be correlated as showing resemblances—family resemblances I mean—with foreign forms. And both of these types had made their appearance, admittedly now here in America, before the close of the Pennsylvanian, one the derivative of Upper Carboniferous, possibly sub-Carboniferous stock, the other a later development, and both continuing for a brief period in Europe during Permian times. Of all the remainder of the air-breathers not one can be compared with forms known elsewhere in the world, save in the general characters, ordinal characters at best.

These facts can mean but one thing, the faunal isolation of land and freshwater vertebrates during all of the so-called Permian times in America. The faunistic evolution here was great, however. At least three very distinct phyla of reptiles and as many of amphibia are known with certainty: the Pelycosaurs (*Naosaurus*, *Dimetrodon*, etc.), derivatives of a prior type which had branched off before the close of the Pennsylvanian; the true Cotylosaurs (*Otocoelus*, *Diadectes*, etc.) with, in some cases, singular developments of dermal carapace, strongly suggestive of the turtles, unknown elsewhere; and a third type (*Labidosaurus*, *Pariotichus*, etc.), for the present nameless, small crawling reptiles with large head, short tail, short limbs, whose nearest, but remote relatives are found among the pareiasaurs of South Africa, doubtless derived from the same common stock as the pareiasaurs, but modified by long isolation. Of the amphibia the most numerous and best developed are those with temnospondylous vertebrae, that is those which have the vertebrae divided into separate elements, the type from which the mammals doubtless eventually arose, as well as the cotylosaurs, and pareiasaurs. This group is also abundantly represented in the Lower Permian of Europe, but reached the highest expression in the Texas Permian (*Eryops*). A second type, represented by a few forms, in America, known from the latter part of the Pennsylvanian throughout the Permian (*Diplocaulus*, *Crossotelos*, etc.) represents sparsely the continuation of the microsaurs

perhaps, but with marked modifications in structure peculiar to the American forms which separate them widely from their Permian relatives of Europe. The third, representing the earliest known type of the modern amphibians (*Lysorophus*), is, so far, entirely peculiar to our Permian, another evidence of isolated evolution. There are no known representatives of the stereospondylous types of *Stegocephalia*, that is the true labyrinthodonts, which, however, as we shall see, suddenly reappear in the Upper Trias, and doubtless were represented in the later Pennsylvanian of this country by known forms from Kansas, and by Marsh's *Eosaurus* from Nova Scotia, etc. Upon the whole, then, our Permian fauna is sharply and almost completely distinguished from any supposed contemporaneous or indeed any fauna known elsewhere, and may have been evolved wholly in America from known Pennsylvanian forebears. The Texas and Oklahoma Permian deposits were undoubtedly for the most part or entirely those derived from extensive flats of slight elevation, deposits composed for the most part of the finest, almost impalpable mud, with little extraneous material, traversed here and there by current channels, and streams which have left for evidence interrupted ribbons of fine or coarse sandstone, and some beds of gravel, with intercalations everywhere of lenticular masses of very fine sandstone of aeolian or quiet water origin. In other words, as has often been said, the deposits are typical shallow freshwater deposits, gradually merging on the north, as Beede has recently shown, into the shallow marine deposits of the Lower Kansas Permian. Few if any real marine vertebrates are known from all these extensive and varied deposits, since the shark and dipnoan remains not infrequently found may have been, and doubtless were, of fishes already habituated to fresh or brackish water. That there may have been in America contemporaneous forms living on the higher lands of which we have yet no knowledge is doubtless true, but not very probable; the higher grounds of the Wichita Mountains on the north have sent abundant gravel and sand material southward into these deposits, and they surely would also have sent some fragments of distinctive high-land creatures with them had there been any. There is, I believe, in all these deposits, not a single hint of the ancestry of modern reptiles save possibly of the turtles and ichthyosaurs. Nor do I believe that there is any evi-

dence of the great phyla of archosaurian and synaptosaurian reptiles here, for I, for one, am pretty thoroughly convinced that the Pelycosaurs have no genetic relationship with either of these groups. The origin of the branch leading to the mammals, so far as our knowledge yet goes, was in Africa; there is nothing to prove that it was in North America. What then became of the Permian land fauna of North America? Not a trace of it is found later in the Mesozoic land fauna of America. Until we know more of the land fauna of South America, during these and later times, it is impossible to say just what became of it, but certainly, with the close of the Permian time, so far as our knowledge yet goes, it was completely blotted out of our records.

How much longer this Permian isolation continued it is of course impossible yet to say, since the gap in our records to the Upper Triassic is complete and absolute, at least so far as distinctively land forms are concerned. Dr. Merriam has brought to light within recent years from the Pacific regions a comparatively rich and varied marine vertebrate fauna of the Middle and Upper Trias, but it does not throw much light on continental faunal conditions. The remarkable demonstration of evolutionary characters presented by the numerous ichthyosaurs which he has discovered indicates, it seems to me, a dispersal center of these animals, a group which must have been derived from the most primitive of reptiles, such indeed as the Permian fauna of America presents; and they may have been the direct descendants of that fauna. With them, moreover, is associated a remarkable new group of reptiles, the thalattosaurs, of almost subterrestrial type, unknown elsewhere in the world, a form which may have arisen from Lower Triassic land reptiles of true rhynchocephalian affinities, the first indication of this type, I believe, in America. Where their ancestors came from we cannot say, but I believe that they were immigrants, since we know of nothing that could have been their progenitors from the Permian of America.

With the land fauna of the Upper Trias of America we have again the most astonishing proofs of an intermingling of European and American faunas, an opening-up of some broad land connection which had been interrupted during Permian times. In the phytosaurs and the nearly contemporaneous thalattosaurs of the Pacific Triassic we have the first definite indication of the great archosaurian group

of reptiles, already represented since early Permian times in Europe. Both they and the associated labyrinthodonts, which had been wholly absent since Carboniferous times, show the most intimate affinities with the European types, proving beyond doubt the equivalency of the deposits yielding them with the Keuper of Europe. And, also associated with them, are true dicynodonts—of this I have no doubt—forms intimately allied to those of similar age in the Trias of South Africa, the first representatives in America of another great group of reptiles, the Synaptosauria. Between the horizons yielding Permian fossils, whether vertebrate or invertebrate, and that affording these Keuper Triassic animals, there are, in both Kansas and the Lander region of Wyoming, at least a thousand feet of continuous, conformable, uninterrupted, and homogeneous deposits of red sandstones, deposits utterly barren of all animal or plant remains. I have asked geologists in vain what such deposits mean. One thing they do mean, for the Rocky Mountain region at least—continuous and uniform physical conditions. What became of the Permian vertebrates during this interval we cannot say, for, as I have said, there is, I believe, not the slightest trace of them or their descendants in the land fauna. And from the east, as also from the west, we get before the close abundant evidence of dinosaurs and aetosaurs; and a peculiar type of mammals, from Carolina.

Again comes a most lamentable gap in our knowledge of land vertebrates in America, that of the Lower and Middle Jurassic. With the Upper Jurassic marine beds, come in the most specialized of the ichthyosaurs and highly specialized plesiosaurs and a single fragmentary specimen of a crocodile, the first from the American continent. Both the ichthyosaurs and the plesiosaurs show such high evolution that we must admit their recent migration from Europe, where indeed a closely related ichthyosaur had anticipated our form and the plesiosaurs had long been known.

With the close of the Jura a rich land fauna appears in the Morrison beds, rich but not varied, composed almost exclusively of dinosaurs, dinosaurs big, dinosaurs small, carnivorous, herbivorous, walking, running, almost flying dinosaurs, of high and low degree, but among them all not a single type that is distinctively American, not one that is not, prior to this time or as a contemporary with it, known

from the eastern continent. *Morosaurus* mimics *Cetiosaurus*, *Camp-tosaurus* *Iguanodon*, *Stegosaurus* *Omosaurus*, *Allosaurus* *Megalosaurus*, etc. We are confident then that during Morrison times there was freedom of migration between the eastern and western continents, so free that nothing distinctive of our fauna had been developed through isolation. Here now we find for the first time meager representatives of the first turtles, of a single type, which had been known on the eastern continent since Middle Triassic times, almost the first crocodiles, well known also there since Triassic times, but represented here by a single form with relatively few individuals, of a distinctively European genus. Nothing else save a single fragmentary bone of what may have been a pterodactyl, and a recently discovered (Gilmore) terrestrial rhynchocephalian, known over there from the Permian, Trias, and Jurassic; not a nothosaur, so characteristic of the European Triassic land fauna, not a lizard, known from the Triassic of Africa, not a bird, known from the Upper Jura of Solenhofen, practically nothing but dinosaurs, and mammals very closely allied to the Kimeridge or Wealden mammals of Europe—the first known multituberculates here, but known from the oölite there. Can one conceive of more favorable conditions for the preservation of the remains of all these creatures and of the small salamanders known contemporaneously in Europe, than those which existed through the thousands of miles of extent of low-lying, marshy lands of Morrison times? It will not suffice to say that we may yet find them in America. Under far less favorable conditions, apparently, bird remains are found in the Upper Cretaceous of New Jersey, Kansas, and Wyoming.

The conditions and faunas of the Morrison times are continuous throughout the Lower Cretaceous, so far as we know them; nothing new, nothing different save the reappearance of the plesiosaurs, nothing strange, nothing distinctive, and no type missing.

With the Upper Cretaceous the meager fauna of the Dakota gives only the footprints of a bird and a more distinctively terrestrial turtle. In the Benton, aside from the marine plesiosaurs, which here reach their culmination perhaps, and the ichthyosaurs, which now are dying out here after their disappearance in Europe, we find the last of the broad-nosed crocodiles (*Coelosuchus*) of ancient type, another

lingerer, which had apparently disappeared in Europe, and the first of the slender-nosed crocodiles of olden type, their first appearance here after their last records from the eastern continent. And with them appears for the first time a new type of dinosaurs, the armored polacanthids (*Stegopelta*) which had appeared in Europe in the Wealden, but which is unknown from the earlier deposits of America among all the vast numbers of dinosaurs. With the close of the Benton and the beginning of the Niobrara, we find the first appearance of distinctive American types of air-breathing vertebrates since the decay of the Permian fauna, save the thalattosaurs of the Pacific Trias, in the large marine turtles (*Protostega*) and the duck-billed dinosaurs (*Claosaurus*). And what is very interesting is the first appearance of the scaled reptiles, the mosasaurs, in America. But the mosasaurs had already reached a high degree of importance in the east and perhaps in the south. They appear here suddenly without any such premonitions as are found in southern Europe, long after their appearance there. Although marine animals, they live near the shores and doubtfully ever braved the oceans; they must have followed the land. The birds, too, now are numerous and of considerable diversity of form; and the pterodactyls swarmed the seas, pterodactyls which had gradually been evolving in Europe till they had reached almost or quite the American specialization in the Cambridge Greensand. What was the cause of their delay in reaching this continent? Certainly not our lack of knowledge of the faunas, for I believe that we can say with tolerable certainty that no pterodactyls were in existence here till the time of the Colorado Cretaceous, certainly none of the Cretaceous type which began in the Wealden of Europe. The plesiosaurs, on the other hand, have taken on specializations which, notwithstanding their supposed freedom of migration, indicate comparative isolation from the European forms, for not a single genus is identical, and, save possibly *Platecarpus*, there is not a single genus of mosasaur quite identical with those of the European fauna. Unfortunately we know little of the land animals of this epoch, but altogether I think we are justified in saying that the freedom of communication between European and American land vertebrates was somewhat restricted.

During the times of the Fort Pierre and Laramie, inclusive of the

New Jersey and Judith River faunas, we get some notable, though very dilatory appearances of European forms, the first land scaled reptiles, the first salamanders, and, with them, the first of the modern type of crocodiles, allied to the Borneo gavials. And with them also, the very much belated long-headed crocodiles of ancient type gave up the ghost, while the duck-billed and horned dinosaurs and the marine turtles, all distinctively American forms, the most distinctive of American Mesozoic vertebrates save thalattosaurs that we have, waxed and grew mighty. A new type for America of terrestrial turtles appeared. The polacanthid dinosaurs, long since unknown in Europe, continued to the very close (*Paleoscincus*). The mosasaurs present a European genus (*Mosasaurus*), but one that was most certainly developed here in America, and emigrated. Finally at the close a new type of reptiles (*Choristodera*), with marked rhynchocephalian affinities, appears both here and in Europe, continuing on into the Tertiary, in forms almost generically identical; and the same may be said of the American crocodiles (*Thoracosaurus*) which reappear in Europe in the early Tertiary, with scarcely any differences.

And all these facts indicate conclusively a continued intermigration between the eastern and western continents of land animals, with possibly some less freedom during late Cretaceous times.

To summarize: The Pennsylvanian fauna has nothing distinctive, at least till near the close; there must have been a continuous and free interchange of land animals with the eastern continent till near the close. Before its close, it had already diverged and certain true reptiles had appeared. Before the beginning of Permian times an interruption of migration occurred, producing a complete and continuous isolation of the Permian American fauna. With the close of these times a long interval elapsed, during which physical conditions were almost uniform over a large part of the Rocky Mountain area at least; during which interval we have no records of land or freshwater life, but which is represented in part by marine forms of remarkable character, possibly in part derived from American ancestors. With the reappearance of land forms in the Upper Trias we find certain evidence of free migrations again, with the closest relationships between eastern and western forms, none of which could have been derived, immediately at least, from the known American

Permian types. The marine vertebrates of the Upper Jurassic, the next American air-breathers of which we have any knowledge, indicate an advance in specialization over the contemporary forms from the eastern continent, but they also indicate a continued migration of the aquatic forms at least. With the land forms again appearing at the close of the Jurassic and in the Lower Cretaceous, we find strong evidence of a community of faunas, but with a striking absence, hitherto, of some of the smaller forms known from earlier times in the eastern continent. The Upper Cretaceous again shows a belated arrival on the western continent of eastern types, after their advent or even disappearance there. With the exception of certain Triassic marine types, we have no distinctively American Mesozoic groups of air-breathing vertebrates, until we reach the Benton, Niobrara, and Pierre Cretaceous, all indicating a continued, but possibly restricted intermigration between the eastern and western continents during the whole of Mesozoic times. In which way did these migrations occur? That the communication between the two continents in Pennsylvanian time may have been by way of the north Atlantic region is not at all improbable. Indeed, taking into consideration the close relationships known to exist between the European and American type of this period, closer perhaps than existed at any subsequent time during the Mesozoic, this more direct way of communication would seem very probable.

On the other hand, the very close relationships existing between the species of the Proganosauria, hitherto found only in South America and Africa, one genus of which is exclusively American while the other genus, *Mesosternum*, according to McGregor's recent observations, is represented in both continents by closely allied species, would suggest a close land communication between the two continents during early Permian times at least. That *Mesosternum* may have reached the two continents, Africa and South America, by the long, roundabout way of the north Atlantic, is hardly possible, for the same freedom of communication would have opened up North America to the ingress and egress of European and American forms. It would seem altogether probable, then, that there not only was a free communication between Africa and South America in Permian times, but that also the communication between North and South

America was closed during the same interval, though of this we cannot be at all sure till we know more of the South American Permian fauna, which, so far, lacks every distinctive form peculiar to North America.

Whether or not the communication between North America and the eastern continents was by way of the north Atlantic, it is quite evident that there must have been free communication during part or all of the Mesozoic time between North and South America, proof of which is seen in the dinosaurs, mosasaurs, and crocodiles, some of them, according to competent observers, identical generically even with North American forms. We have yet much to learn about the Mesozoic fauna of South America, but, so far as our knowledge yet goes, there is a close relationship between them. This similarity, of course, may have been the result of a westward migration from Africa to South America by the way of a southern land communication, and a concurrent intermigration of the same types from Africa northward to Europe and thence by the north Atlantic to North America. But a simpler explanation would be that of a land communication between North and South America, and a single trans-Atlantic bridge, which, in my opinion, was the southern one.

It is very true that such hypotheses as I have offered are largely based upon negative evidence. Future discoveries may bring to light, both in Europe and America, types which now appear to have a more restricted geographical distribution; especially may future discoveries in South America and Africa show more distinctive types, or, on the other hand, more common forms. I do believe, however, that the long-continued exploitation of the Mesozoic rocks of North America is gradually converting negative into positive evidence; that we may say with tolerable certainty that certain types of land vertebrates, such as the Proterosauria, Proganosauria, Pareiosauria, Therodontia, etc., have never existed in North America.

In the accompanying table I have given, as fully and as accurately as the present state of our knowledge will permit, the geological range and distribution of the larger groups of air-breathing vertebrates, with especial reference to North America. In not a few instances precise stratigraphical data are wanting, so that groups must be recorded throughout a division of the chart, which later may be found to have a more restricted range. An attempt has been made to indi-

cate by association the phylogenetic relationships of the groups, but it must be remembered that opinions differ not a little concerning the phylogeny of the reptiles, and those expressed in this chart are merely the ones which seem most reasonable to myself. I am indebted to Dr. v. Huene for a number of suggestions and facts of distribution which have been incorporated in the table; and to Dr. W. D. Matthew I am also obliged for the data for the mammals. It is to be hoped that Dr. Matthew will confer a favor upon us all by publishing soon a complete table of the distribution and range of the mammals; no one is more competent.